NESTING ECOLOGY OF BANK SWALLOWS IN INTERIOR ALASKA

A

THESIS

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NESTING ECOLOGY OF BANK SWALLOWS

IN INTERIOR ALASKA

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ABSTRACT

Nesting ecology of bank swallows (Riparia riparia) was studied on Eielson Air Force Base, Alaska, during the summers of 1977 and 1978. The primary objective was to conduct preliminary surveys in to the various phases of the bank swallow's nesting ecology in Alaska.

Observations were made at 11 colonies ranging from 7 to 204 active burrows. Mean length of burrows varied between colonies. The overall mean burrow length averaged 64.4 cm (S.D. = ± 19.7) for 512 burrows. For 242 nests mean clutch size averaged 4.09 ± .78 eggs.

Within a colony, laying, hatching and fledging were synchronous among members. Swallows also capitalized on group behavior by social foraging and mobbing predators.

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INTRODUCTION

The coloniality and behavior of the bank swallow (Riparia riparia Linnaeus) has received considerable attention in the past, particularly in the northcentral and northeastern United States. However, there has been little work done in the western portion of their range, including Alaska. Their habit of nesting in colonies, some of which number in the hundreds of pairs, makes them readily accessible for study. The main problem in bank swallow studies is the hidden nature of the nests which prohibits direct observation of many breeding activities. The large numbers of closely nesting individuals, in addition to the similarity of sexes, make other observations difficult. This is further complicated by the short stay of bank swallows in Alaska, which necessitates compressing many activities into only a few days.

The bank swallow usually nests in natural deposits of soft soil or gravel. Road cuts, stream banks, gravel quarries, and natural escarpments are popular sites in Alaska. Sawdust piles may also provide nesting sites as noted by Bent (1942):

> A departure from their nesting in banks of natural deposits is the use of sawdust piles left by lumbering operations. On June 6, 1902, Barrows saw from a train large numbers of Bank Swallows about sawdust piles at Ostego Lake,

> Michigan. Bradford Torrey (1903) reports observations of Mrs. Annie Trumball Slosson made at Franconia, N.H., in the summer of 1902. She saw no less than 20 holes that had been excavated in a sawdust pile, and apparently all were occupied by the swallows, which were carrying on their usual activities entering and leaving the holes as at any other colony.

Cox (1961) and Greenlaw (1972) reported swallows in sawdust. Bent (1942) also reported ". . . bank swallows nesting abundantly in the walls of an abandoned dry well about 15 feet deep. The perpendicular walls were honeycombed with the nesting holes." In addition, swallows have been recorded nesting in stonework (MacNeill 1954), walls (Sudhaus 1970), gravel pits (Stoner 1926), coal piles (Spencer 1963) and drainage holes or pipes (Hickling 1959 and Williams 1967). In fact, colonies in Alaska are very frequently found at man-made sites. In a study by Spencer (1963) of bank swallows in Vermont and Pennsylvania, 4 of 25 colonies were in man-made sites. All colonies in this study were in man-made sites.

OBJECTIVES

The major objective for this study was to conduct a broad preliminary survey of the nesting phenology of bank swallows in Alaska. This was accomplished through the following secondary objectives:

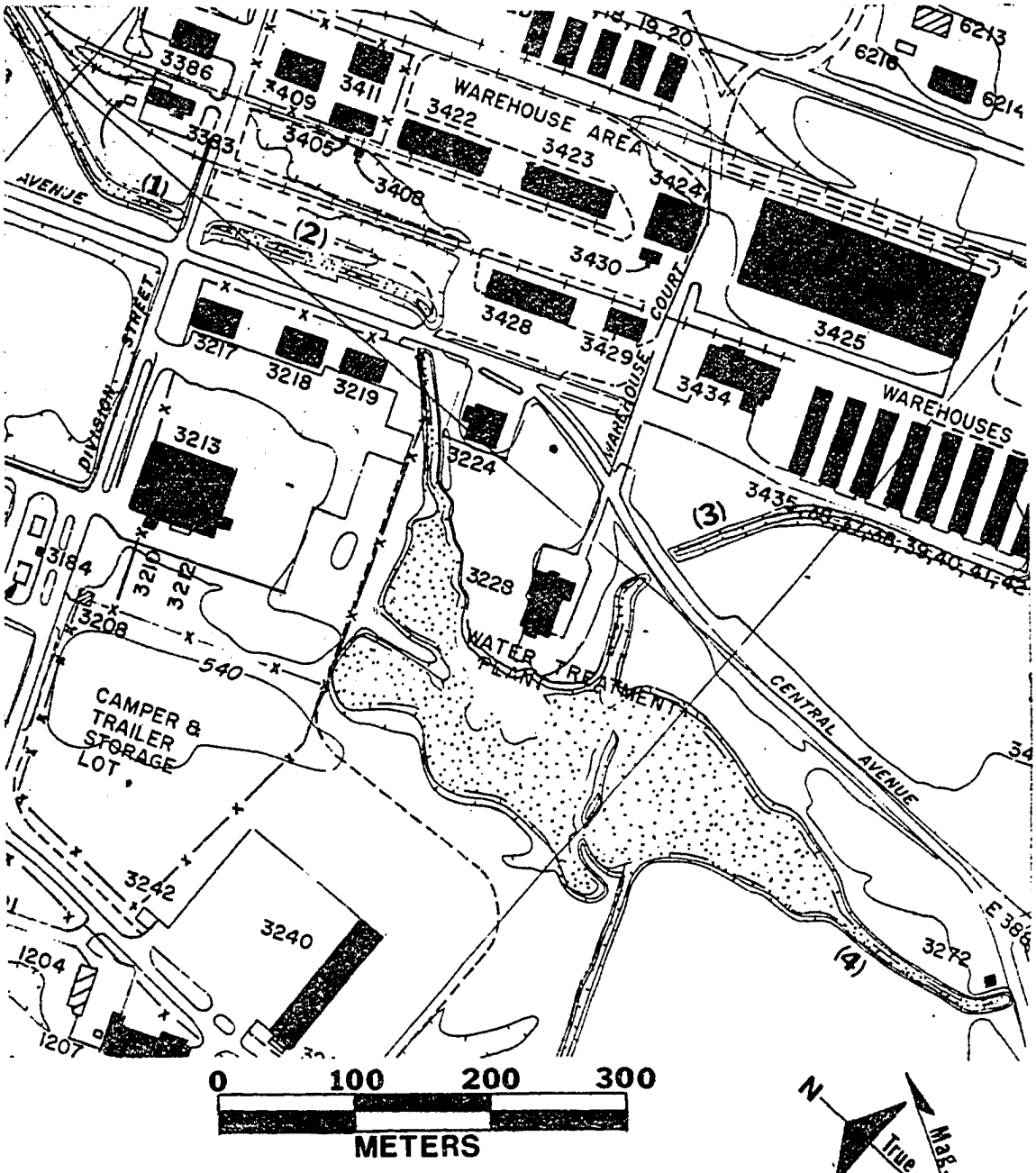
1) Observe and describe as many factors relating to nesting phenology as possible.
2) Determine and describe the method, extent and rate of burrow excavation.
3) Determine clutch size.
4) Gather further behavioral information on pair formation, care of eggs, care of young, and juvenile behavior.
5) Determine the extent and effects of mobbing.
6) Document evidence of predation.

METHODS

General Observations

In early May of 1977, 11 old bank swallow colonies were located on Eielson Air Force Base (AFB), approximately 40 km south of Fairbanks, Alaska (Figures 1, 2, 3, 4). Prior to the arrival of the swallows, burrow entrances were mapped, and measurements were taken of as many burrows as possible. Five of the colonies were in very fine soil deposits, four colonies were in compacted coarser soils along stream and lake banks, one colony was in a moderately graveled soil in a ditch, and the last colony was in a pile of construction gravel. Additional colonies were also located on Eielson AFB and used for supporting data, but were not studied in detail. Studies in 1978 were generally limited to three of the larger colonies. Visits were made to the other colonies for incidental observations.

The colonies ranged in size from 7 to 204 active burrows. As a rough estimate, this relates to two adult birds per burrow for an adult population of from 14 to 408 individuals. During 1977, attempts were made to visit all colonies at least twice a week from the end of May until departure of the swallows in early August. With fewer colonies in 1978, observations were made at least every



KEY TO COLONIES

(1) RAILROAD (2) SUPPLY (3) WATER PLANT (4) TOWSA

FIGURE 1. Map of portion of Eielson AFB showing Railroad, Supply, Water Plant, and TOWSA colonies.

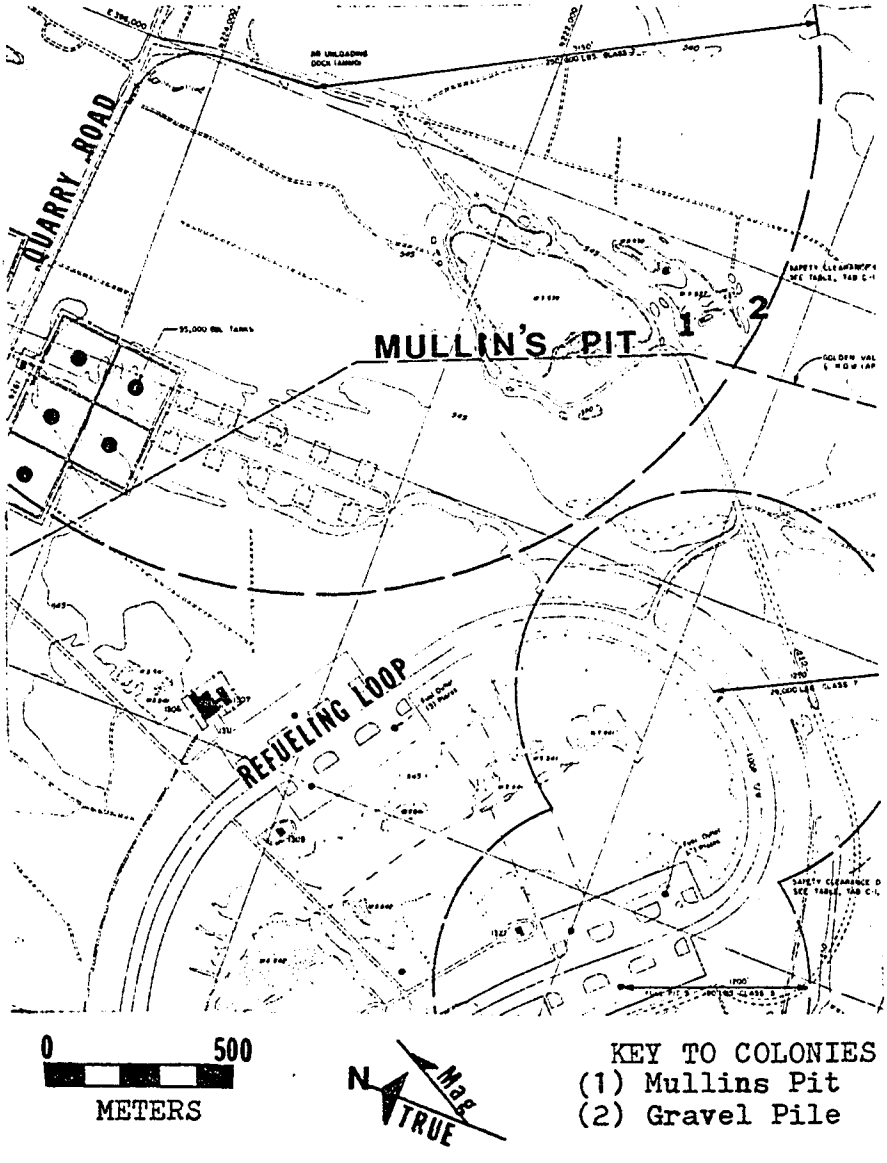


FIGURE 2. Map of portion of Eielson AFB showing Mullins Pit and Gravel Pile colonies.

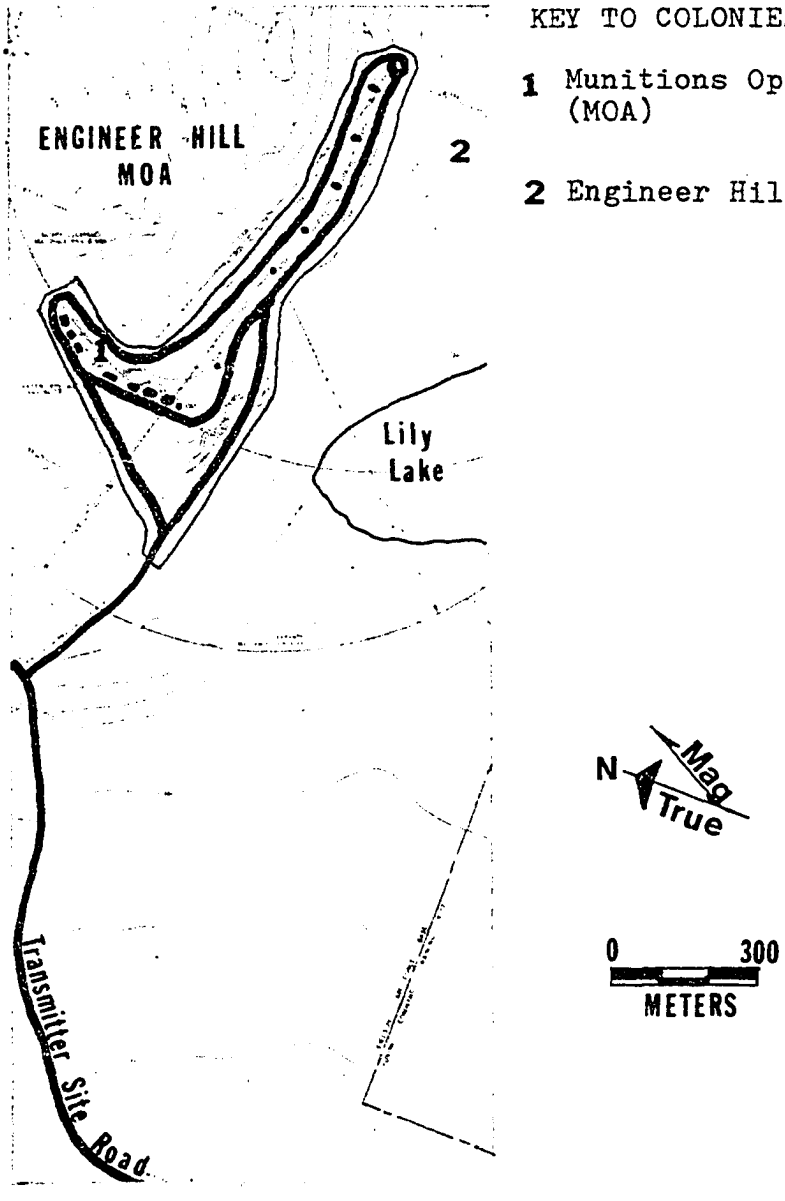


FIGURE 3. Map of portion of Eielson AFB showing Engineer Hill and Munitions Operating Area colonies.

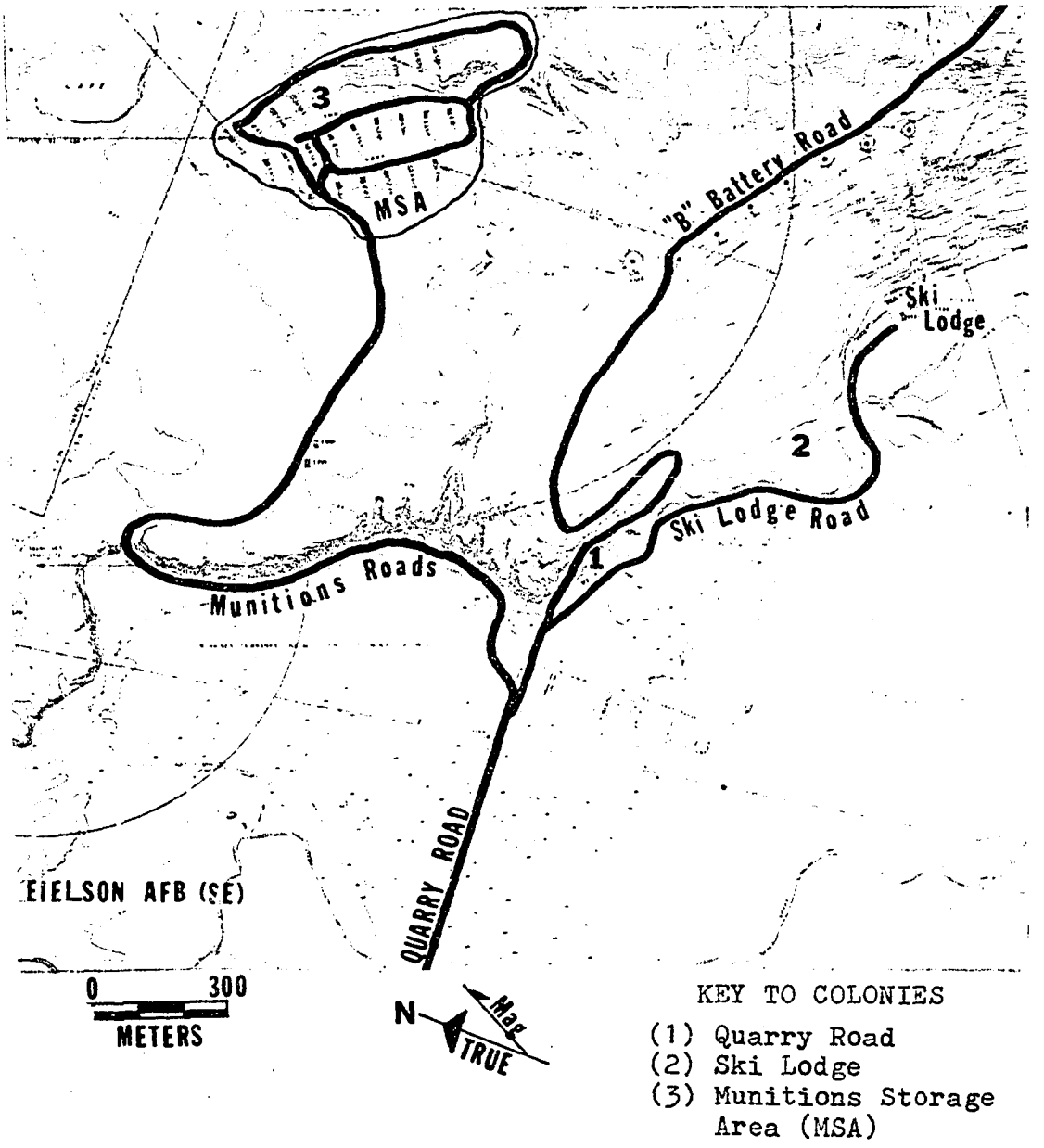


FIGURE 4. Map of portion of Eielson AFB showing Quarry Road, Ski Lodge, and Munitions Storage Area colonies.

other day. During the 1977 season human disturbances were kept to an absolute minimum except in one colony. In 1977 there was concern that these disturbances would alter behavior or cause abandonment of the site. However, previous observations indicated that the birds were tolerant of most human activity. This was especially true as the nesting season progressed. Therefore during 1978 work was undertaken actively at all colonies. However, visits by the investigator to colonies were limited to no more than one and one-half hours.

A scale map, with a grid, was used to plot all burrow entrances, following the method used by Petersen (1955). Each entrance was given a number and letter identification (Figure 5). If more than one burrow occurred in a grid, subletters were added. Additional copies of the maps were reproduced and used for making subsequent observations. After arrival of the swallows, observations and examinations of the burrows facilitated determination of the active nests. In addition, since colonies were mapped and measured prior to the arrival of the birds; new burrows were recorded during each visit by the investigator, and measurements of maintenance activities made. This was possible even though the maintenance activities may not have been observed directly. Burrows were also marked by scratching numbers near them in the soil or by using numbered stakes for quicker reference.

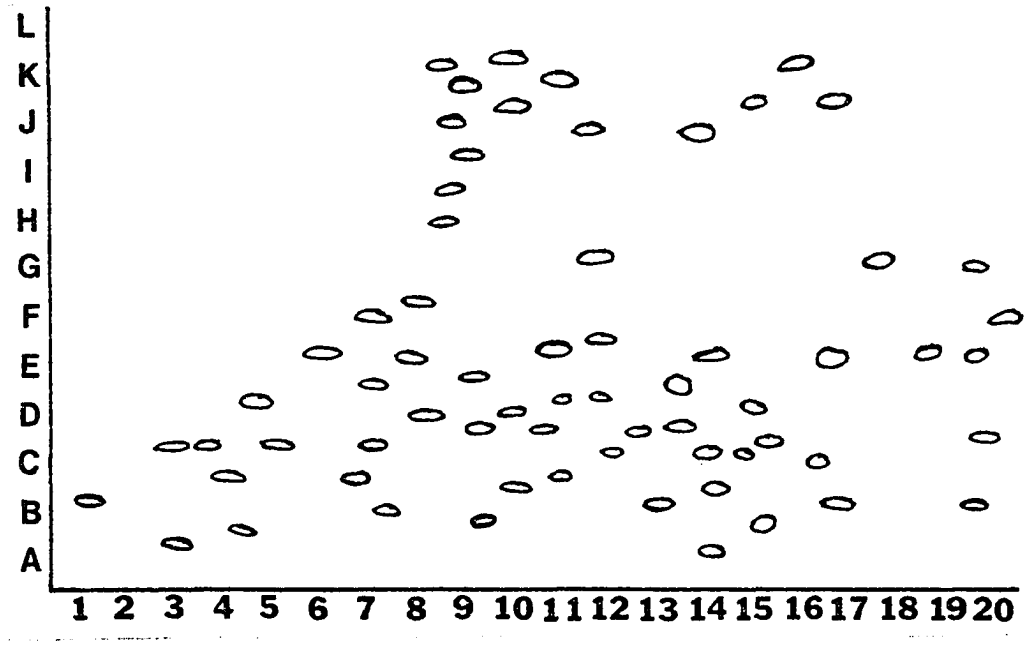


FIGURE 5. Map of bank swallow burrow entrances illustrating the method of identifying burrows. Method adopted from Petersen (1955). Map shows the first 6 m of Quarry Road colony in 1977. Each grid is 30 cm square with holes on the grid being of approximate size.

Viewing of Nests

Several observation methods were tried for viewing nest contents. A flashlight was used to look into nesting burrows. However, depth of the burrows and the surrounding nest materials made it extremely difficult to accurately observe all eggs. Next a small swivel mirror was fastened at an angle to a 92 cm dowel and used in the burrow. This method also had several drawbacks. Deep burrows were too dark to see in without a light. When a flashlight was used it usually reflected back off the mirror or did not fully light the nest interior. In addition, holding a light at the small burrow entrance, along with the dowel sticking out, left little room for viewing. This was an extremely awkward method of observation usable in only a few of the burrows.

Development of a better observation method was necessary. Nests were viewed satisfactorily using a telescopic car radio antenna with a small swivel mirror mounted on the end. For illumination a flashlight bulb was attached approximately 5 cm in front of the mirror and wired to a 6 v battery pack worn on the belt around the waist. The telescopic rod allowed easy observation in the burrow without a protruding dowel. By pushing the mirror against the nest wall the angle could be adjusted for viewing. This simple device proved to be extremely valuable in nest observations.

Viewing Pit

To observe activity at the nest, a viewing pit was dug directly over one nest chamber (Figure 6). In the bottom of the pit a piece of glass was placed over the nest chamber. This allowed direct observation of the nest. When not in use a plug with approximately 10 cm of dirt was placed on the glass. Then a board was placed over the hole further sealing it. By removing the board and the plug the nest could be observed directly. If the observer placed a tarp over himself and the pit all outside light could be blocked while making observations. Just enough light would then enter through the burrow entrance to make the occupant barely visible. This also hid the observer from the birds, thus allowing them to return to the nest and carry on normal activity. Observations were scheduled in early morning, midday, and evening.

Marking and Banding

After the egg-laying period, individual birds were caught, by hand or in mist nets, and marked. Birds were marked (as described by Hoogland and Sherman 1976) with yellow, green, red, and brown felt tip markers. The colors were applied in various combinations to either the right or left half of the breast. Svensson (1969, cited by Hoogland and Sherman 1976) and Oring and Knudson (1973),

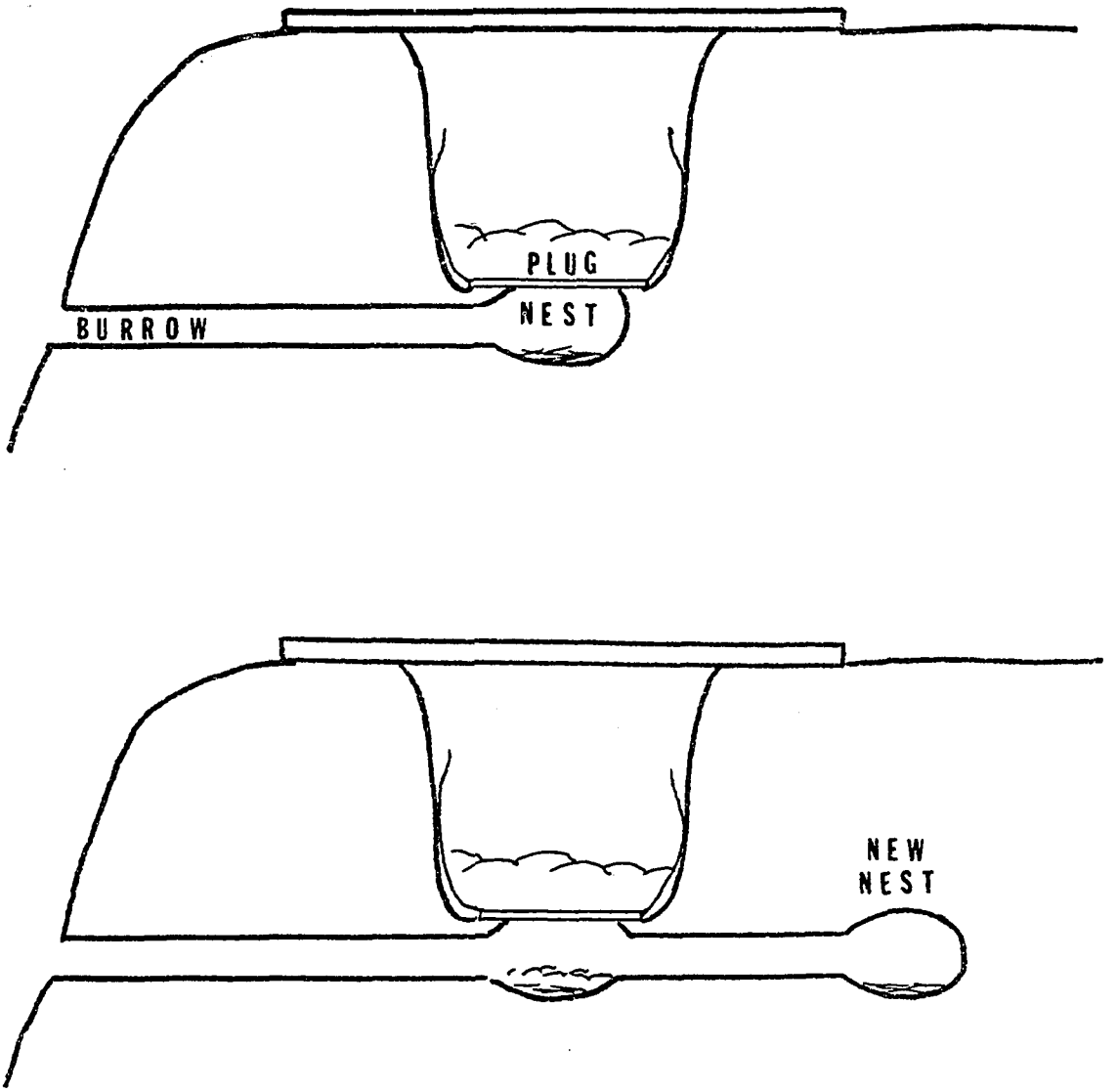


FIGURE 6. Viewing pit constructed directly over bank swallow nest cavity showing burrow extension and new nest cavity. Eielson AFB 1978.

used very similar marking methods with different patterns. They divided the bird's breast into quarters applying different colors to both the anterior and posterior halves. They were then able to increase the total number of color combinations available for observation. This method of breast marking worked well for identifying birds at the nest and while birds were flying directly overhead. Problems did occur when birds flew and entered the nest quickly, thus keeping their breast hidden, or if they flew other than directly overhead. When mixing colors in a colony, such as blue and green or orange and red, the colors would be indistinguishable at a distance or while the bird was flying.

Another less satisfactory method of marking, described by Petersen (1955), was also tried. The captured birds were marked by painting the end of the outer primary with enamel model airplane paint and allowing time for the paint to dry. The tips of the seventh and eighth primaries also had to be clipped to expose the colors. This method was improved by using spray cans of enamel paint. With spray paint the tips of all outer primaries were colored, no clipping was necessary, and the paint dried more quickly. This did not allow for a great number of color combinations and was used when only a small number of birds were to be marked. Care also had to be exercised when using the spray paint. If too much paint was applied

over too wide an area, it impaired the bird's flying ability. This was especially true while the paint was wet. During the first season fluorescent orange spray paint was used on the outer primaries and proved to be highly visible. During the second season green and red were also used satisfactorily.

In 1978, 255 adult and juvenile bank swallows were banded with U.S. Fish and Wildlife size 0 leg bands. This was done to further identify specific individuals within and between colonies. This would also be used to identify individuals returning in subsequent years. Seventy-five of these banded birds were color marked as previously described.

Mobbing Models

Several methods for observing mobbing behavior were used. Reactions to an avian predator were tested using a lifesize model of a merlin (Falco columbarius) manufactured by the Ariel Company. The model is in the flying position with wings spread and the legs stretched down. The model was hung by thread from a pole placed over the colony and at various distances from it. A small dog was used as a mammalian predator. It was "staked" out at the colony to elicit mobbing behavior.

RESULTS AND DISCUSSION

Pair Formation

The first swallows observed at any of the study colonies were sighted on 30 May 1977 and 23 May in 1978. This corresponds to Kessel and Gibson's (1978) records of mid to late May arrival dates for bank swallows in central Alaska. Upon arrival at the nesting area the birds showed little sign of social bonds. The birds spent most of their time investigating old burrows and clinging or sitting on the sides of the colony site. Large numbers of birds were also observed flying in circles within 100 meters of the colonies. At this time trips to the burrows were frequent but of very short duration. Usually the bird would enter the burrow, seeming to travel its length; emerge again, pausing for a few seconds at the entrance; then fly away. This whole process took no more than 10 to 15 seconds.

In England, Hickling (1959) observed that flocks of feeding sand martins (bank swallows) participated in a considerable amount of aerial chasing in groups of two, three or more birds. This behavior took place early in the "season" and seemed to be merely the response of birds to others flying away. He stated that it is a casual or random kind of activity; and if an individual bird is

followed, it changes partners frequently. The change may sometimes be the chasing bird and sometimes the bird being chased, moving from one group to another. However, this becomes an important form of display later in the season, changing from a mere pursuit flight to a sexual chase.

Within a few days, pursuit and then sexual flights increased. At this time all the birds seemed to be primarily engaged in these flights and burrow investigations. In pursuit or sexual flights, one bird would maintain close pursuit of another bird in a number of intricate aerial maneuvers. It was also common to see three birds engaged in this activity. Petersen (1955) stated that the female is being chased by the males during these flights. He said, "I have observed sexual chase 10 or 15 times in marked pairs in which the sexes were known and found that in every case the female flew ahead of the male." The sexual flights may originate from the burrow or in flight, but usually ended at the burrows. This observation by Petersen seems to be inconsistent to Hickling's (1959) observations of British sand martins which changed partners frequently.

During courtship the birds were also actively entering and investigating the burrows in pairs and would often enter more than one burrow. Petersen (1955) stated that, "Birds entering burrows other than their own usually showed certain hesitancy of manner contrasting with the

deliberate action of a bird entering its own burrow." In this study entry of neighboring burrows was observed on several occasions and these visits were of very short duration. Usually another bird came to defend its burrow from the intruder, who retreated. The defender hovered near the intruder and directed a loud coarse twittering or buzzing toward the intruder. Eventually pairs selected a burrow of their own and continued to defend it.

Bank swallows demonstrate a very strong synchronization of behavior during the nesting season. Several times when arriving at a colony it was difficult to find even a single bird. Virtually the entire colony was out feeding together and absent for considerable periods of time. At other times many birds were back, excavating burrows, or participating in sexual flights over the colony. Whatever the activity during the courtship period, it is uniformly engaged in by the majority of the colony. This is further verified by Hickling (1959) and Hoogland and Sherman (1976). As Emlen (1971) stated:

> However, colonies are much more than passive aggregations of birds as is evidenced by . . . the presence of frequent group flights and mutual displays throughout the breeding period, and the precise synchronization of nesting activities within a colony (but not between adjacent colonies).

Burrow Excavation

According to Hickling (1959) "Full organization and synchrony are reached as the climax to a period of complex social displays of which burrow excavation is an important feature." Many burrows were observed during excavation and burrow maintenance or rehabilitation behavior occurred in all of the study colonies. The best description of the excavation activities is given by Beyer (1938):

> Both birds of a pair took part in the work. A bird would begin by clinging to the vertical face of the bank with feet and tail and pecking at the dirt with a side-to-side motion of the head. When the opening was deep enough for it to get partly inside it would use its feet also, kicking the loosened sand backward in vigorous little spurts. As the tunnel became deeper the bird disappeared from sight, but still the sand came spurting out as evidence of the work of the little miner inside.

Forbush (1929) stated that dirt is carried out in the mouth. However, this was not the case in any of my observations, nor those of Petersen (1955). Forbush and May (1955) stated that:

> When the birds arrive they retire at night to sleep in their last year's holes, or they quickly excavate new ones, far enough into the bank to give them shelter for the night.

This type of behavior was never observed at any time during this study.

Hickling (1959) described communal excavation by British sand martins. He stated that,

> At one display, a group of birds--three or four commonly, but quite often five or six--may be seen to be active at one hole while neighboring holes are left unattended. During the next display, quite different holes may be used for excavation. Up to three birds often enter one hole to dig, and there may be other birds sitting at the entrance ready to take the place of those already in the hole. Again, birds may be watched moving from hole to hole excavating at several in succession.

This behavior was never observed in my study colonies. In fact, the burrows under excavation were defended by the resident pair of swallows. Excavation at a burrow site was by the pair and no others. This is also as described by Bent (1942), Beyer (1938), Hoogland and Sherman (1976), and Petersen (1955). Usually only one bird worked at a time, occasionally however, both birds attempted to unsuccessfully dig together in the cramped space.

Progress in burrow excavations was kept for five burrows in soil deposits and for two in the gravel during 1977. However in 1978, progress was kept for 195 new burrows in soil and 24 in the gravel (See Tables 1 and 2). In all of the colonies, partially excavated burrows were found that were never completed. Evidence of obstructions were noted in many abandoned burrows. Usually a large rock blocked the way to further excavations. Of the 219 excavations followed in 1978, 53 were eventually abandoned. An excavation was not recorded unless it was greater than 10 cm. There were a large number of minor "scratchings" or excavations of only 3 to 5 centimeters. These were all

new excavations, and they were started and abandoned so quickly that it was difficult to keep track of them. There were so many other measurements to take at this time that recording of those under 10 cm was discontinued.

Throughout the following discussion of burrow dimensions, clutch size, and other counts or measurements means are reported with one standard deviation.

Table 1. Progress in burrow excavation, measured in centimeters during 1977. Measurements show cumulative total length each day.

Date	Burrow 1	Burrow 2	Burrow 3	Burrow 4	Burrow 5	Burrow 6	Burrow[1] 7
3 June	8	5	15[2]	5	10		3
4 June	10	20	30	8	23	3	6
5 June	20	38	43	23	36	8	13
6 June	36	51	23	36	50	15	18
7 June	50	61	69	50	62	20	25
8 June						Aborted	
9 June	71	76	71	77	71		37
10 June	74	79	71	77	74		41
11 June	74	79					41

[1]These nests located in gravel pile.

[2]Digging begun prior to observations.

Table 2. Rates of excavation for new burrows on Eielson AFB in 1978.

Colony	Relative Soil Type	Sample Size	Average rate of excavation (cm) per day ± SD	Longest excavation in one day (cm)
Gravel Pile	Gravel	24	2.7 ± 1.4	13
Railroad	Coarse Compact Soil	76	10.0 ± 8.9	34
Quarry Road	Compact Fine Soil	74	8.3 ± 5.5	23
Supply	Coarse Soil with Gravel	19	12.8 ± 10.7	42
TOWSA	Fine Soil	12	9.4 ± 8.2	36

In all of the colonies studied new burrows were built and some of the older burrows were not utilized (Table 3). As an example, during 1977, one colony, 122 m southeast of Engineer Hill on Eielson AFB, had 120 completed burrows. Most of these burrows were measured prior to the arrival of the birds. The birds never used 12 of these burrows. They excavated 15 new burrows, started and abandoned four burrows, and enlarged four of the previously measured burrows. After establishment of the colony there were 123 active burrows. The burrows which had been enlarged ranged from 23 cm to 41 cm in length prior to arrival of the birds. These burrows had either never been previously completed or had been shortened by shearing of the cliff face. After reexcavation they were from 61 cm to 79 cm in length. Burrows in other colonies were not measured prior to arrival of the birds and reexcavation attempts were not documented. Prior to the 1978 season, larger numbers of burrows were destroyed from caving-in or shearing of the cliff face than in 1977. This is a continual phenomena year after year with varying rates of destruction. This made it extremely difficult to determine active life of burrows from year to year.

Colonies from which measurements were made were never reestablished. There were two in 1977 and one in 1978. One of those in 1977 had been last used in 1975 and the other in 1976. There was no apparent evidence indicating

Table 3. Burrow data for all bank swallow colonies studied on Eielson AFB in 1977 and 1978.

Colonies	Old Burrows Remaining from Previous Year	Burrows Greater Than 10 cm Started and Abandoned	Active Burrows Destroyed During Cycle	Burrows Never Used	New Burrows	Total Active Burrows
Engineer Hill 1977	120	4	1	12	15	123
Engineer Hill 1978	76	3	4	24	1	53
Gravel Pile 1977	15	18	3	7	2	10
Gravel Pile 1978	9	15	7	6	4	7
Railroad 1977	86	11	0	4	29	111
Railroad 1978	92	23	19	6	53	139
Quarry Road 1977	160	10	0	5	22	177
Quarry Road 1978	124	12	0	20	62	176
Supply 1977	-	2	0	1	-	18
Supply 1978	11	1	4	2	18	27
TOWSA 1977	51	2	0	3	10	58
TOWSA 1978	53	2	0	5	12	60
Water Plant 1977	12	2	0	1	2	13
Mullins Pit 1977	24	3	0	1	4	27
Ski Lodge 1977	27	4	0	2	5	29
Munitions Storage Area 1977	42	9	2	4	8	46
Munitions Operating Area 1977	22	5	1	3	4	23
Column Totals	924	126	41	106	251	1097

why the birds never returned to these two areas. In several other areas old unoccupied colonies were also found. However, there is no indication of what the active life of a colony may be. Within the previously abandoned colonies, there was no sign of predation. All the areas were close to human activity, but there had been no apparent disturbance or increase in activity, and the activity had existed in the area in previous years.

In many cases, burrow entrances were so close together that the tunnels would intersect each other. In all cases examined only one of the tunnels would continue on. Hoogland and Sherman (1976) found this coalescence of tunnels to be the case in less than 3% of the 3,000+ burrows they studied. They also found that ". . . in every case, only one pair of swallows remained after the coalescence." Petersen (1955) further confirms this with similar findings. However, Bent (1942) stated that "Merrill (1881) found three burrows that joined in a colony examined on the Cranberry Islands, Maine, each of which contained two nests and all nests contained fresh eggs."

Throughout the period of excavation and nest building territorial disputes occurred. The combatants usually began fighting at the burrow entrance and ended up on the ground below or in aerial combat. This behavior is further confirmed by Beyer (1938), Bent (1942), and Hoogland

and Sherman (1976). Hoogland and Sherman (1976) found that in 44 of these conflicts, begun at the edge of a burrow, 31 (70%) ended in aerial combat, and the remainder terminated on the ground. The frequency of the defense is much greater in the early states of excavation, as territorial boundaries are not yet well established. As reported by Petersen (1955), it was found that both territorial defense and digging were shared, since in many instances both birds were engaged in these activities simultaneously.

In the colony at the gravel pile, 18 abandoned and 10 active burrows were recorded in 1977 and 15 abandoned and 7 active in 1978. This was a rate of 34% of burrows begun and actually being utilized in the gravel pile. In comparison, approximately 91% were utilized in the colonies located in the soil deposits. Both Hickling (1959) and Stoner (1937) said that there are many more burrows excavated than are used for nesting. There were 17 active nests in the gravel colony, and their mean depth of 36.3 ± 4.7 cm was considerably less than the 64.6 ± 15.8 cm mean for the other 495 burrows measured (Tables 1, 2, 3 and 4). Hickling (1959) stated that the "material in which the hole is dug has an undoubted influence on length, and Petersen (1955) found a positive correlation between length of hole and the percentage of sand in the soil." Hickling went on to say however, that he found even bur-

rows dug in a very close group of 11 holes showed a variation of 36 cm to 79 cm.

In this study, a great variation was also found within the same area. In a portion of one colony ten active burrows in a 3 m row of bank ranged from 43 cm to 132 cm with a mean of 85.1 cm. Coincidentally, the 43 cm burrow was located within 15 cm of the 132 cm burrow.

In the gravel pile colony large concentrations of gravel, containing a very fine soil filler, were definitely a deterrent to adequate burrow excavations. The wasted energy in abortive excavations and the extremely shortened burrows must have had a deleterious effect on the colony. For one thing, the shortened burrows made the colony much more vulnerable to predation. Secondly, the nature of the material made it much less stable and "cave-ins" were more evident. During 1977, all but three of the nests were destroyed, and in 1978 all seven were destroyed by man extracting the gravel. In both instances, all the birds abandoned the area and could not be located. These birds could not have continued to use this site and survived as a population.

Table 4. Active burrow and nest cavity measurements at Eielson AFB in 1977 and 1978.

	Total Active Burrows From Colonies Sampled		Sample Size		Mean Length ± SD (cm)		Largest (cm)		Smallest (cm)	
	1977	1978	1977	1978	1977	1978	1977	1978	1977	1978
Burrow Length										
Total	374	462	106	406	67.1 ± 20.4	64.0 ± 19.5	107	137	31	28
Soil	364	455	96	399	68.6 ± 16.8	63.6 ± 15.6	107	137	42	30
Gravel	10	7	10	7	36.8 ± 4.8	35.6 ± 4.6	43	43	31	28
Total Both Years			512		64.4 ± 19.7					
Nest Cavity										
Length			20	20	16.8 ± 2.2	17.1 ± 2.3	22	20	13	13
Width			20	20	11.5 ± 1.5	11.5 ± 1.5	17	17	6	6
Height			20	20	8.9 ± 1.2	8.6 ± 1.1	13	12	5	5
Total Both Years for Nest Cavity										
Length			40		16.9 ± 2.2					
Width			40		11.5 ± 1.5					
Height			40		8.7 ± 1.1					

Burrow Data

The average burrow was 6.4 cm wide and 3.8 cm high, with rounded sides and bottom and a flat ceiling. With time the entrances became enlarged and vertically elongated due to the erosion caused by use. The burrows usually ran straight back with a slight upward slope that was hardly noticeable. Beyer (1938) stated that ". . . usually the burrow slopes slightly upward or bends gently upward a few inches back from the entrance." This was also mentioned by Bent (1942). However, this upward bending was only slightly noticeable in the majority of burrows that were examined.

The 512 burrows that were measured ranged from 28 cm to 137 cm with an average length of 64.4 ± 19.7 cm (Table 4). Hickling (1959) found a range of 36 cm to 119 cm. Occasionally tunnels would be found that turned slightly to the side, downward, or upward. However, this was usually due to a detour around a rock. Stoner (1936b) observed that burrows started earlier in the spring tend to be longer than those started later, especially if they are in soft sandy soil.

Varying mean lengths of burrows are reported by different authors. In fact, mean lengths were considerably different for each colony studied. As an example of four colonies in soil, during 1978, the mean lengths from samples were 82.2 ± 20.1 cm for 57 burrows, 67.8 ± 7.2 cm

for 27 burrows, 65.0 ± 19.2 cm for 139 burrows and 55.8 ± 12.6 cm for 176 burrows with a combined mean and ± one standard deviation of 63.6 ± 15.6 cm. Hickling (1959) reports an average length of 65.53 cm for 29 burrows and Stoner (1937) had 71.12 for 89 burrows. In fact, there is even great variation within a colony. Hickling (1959) believed that the length of the hole is not what determines when nest building begins. The only requirement would be that a minimum length of around 30.5 cm be met.

The difference between the varying lengths within and between colonies is related to when they were begun. In both years, for all colonies sampled, the digging period lasted from five to seven days. It has been suggested that the earlier individual holes or colonies are begun, the deeper the burrows. In 1977 all colonies had digging start within two days of the first colony to dig. In 1978 they all started within one day of the first colony to begin digging. Length of burrows begun later decreases rapidly, possibly as the birds sense impending ovulation. The time of excavation and nature of the soil are the factors determining length of burrows. There is also some speculation that younger inexperienced birds dig shorter burrows. Burrow lengths are listed variously by other authors (Table 5).

Table 5. Range of bank swallow burrow lengths and means in other studies.

Source	Length (cm)	Mean (cm)
Hickling (1959)	35.56 to 119.38	65.53
Stoner (1937)	38.1 to 119.38	71.12
Spencer (1963)	25.4 to 101.6	58.92
Bent (1942)	longest 121.92 in sand; shortest 35.56 in clay and pebbles	48.26
Stoner (1936b)	least was 40.64 or 45.72 usually 55.88 to 91.44; deepest burrow was 165.1	71.12
Palmer & Fowler (1975)	38.1 to 243.84	
Berger (1961)	60.96 to 91.44	
Beyer (1938)	109.22 longest	about 76.2
Forbush (1929)	38.1 to 244 or more (same as Palmer & Fowler 1975)	
Petersen (1955)		51.82 to 91.95
This Study	28 to 137	64.4 ± 19.7

In one study by Petersen (1955) 10 sites in 8 colonies were studied in Wisconsin. He used the hydrometer method (Taylor 1948) to analyze the soil textures. His data showed a positive relationship between the percent of sand in the soil and the mean burrow length (See Table 6).

Table 6. Soil texture and lengths of bank swallow burrows reported by Petersen (1955)

Colony	Mean Burrow Depth (cm)	Soil Texture		
		percent sand	percent fine material	Class
Wisconsin River, Area 1.....	91.95	92	8	Sand
Wisconsin River, Area 2.....	83.82	91	6	Sand
Columbia Co. V. Road cut.....	72.39	93	7	Coarse Sand
Black Earth Creek, sandy layer.....	65.02	91	6	Coarse Sand
Black Earth Creek, loamy layer.....	56.39	85	15	Loamy Sand
Dane Co. Hwy. Q. Sand pit....	54.86	85	15	Loamy Sand
Monona Road cut, lower layer.....	53.85	83	17	Loamy Sand
Monona Road cut, upper layer.....	51.05	80	20	Loamy Sand
Nine Springs Creek.....	52.58	75	25	Sandy Loam
Sprague-Dawley pit.....	67.31	65	35	Sandy Loam

Measurements were made of soil banks at four colonies. In all cases the majority of the bank appeared to be suitable for burrows. However, swallows only utilized a portion of the available area. Stoner (1936), Petersen (1955), Spencer (1963), Emlen (1971), and Hoogland and Sherman (1976) reported similar findings. The linear amount of bank presumably available for burrows and the

amount actually used was measured. In these apparently suitable areas the percent of utilization ranged from 4% to 46% with a mean of 26% ± 15%. This suggests that the birds clump their burrows rather than distribute them uniformly when suitable space is available.

To test whether burrows were randomly distributed or clumped, the nest grid map was divided into cells. The observed cell frequencies were the number of active burrows falling into each cell. The critical value of chi-square at the .05 significance level showed that burrows were clumped and that there was a definite preference for higher nests. This was also reported by Stoner (1936), Petersen (1955), Spencer (1963), Emlen (1971), Hamilton (1971), and Hoogland and Sherman (1976).

Nests

The nesting cavities are located at the terminal end of burrows. The cavity is enlarged upward and to the sides with the floor of the burrow and floor of the nest cavity being on the same level. The nest itself is a shapeless mat composed mostly of dried grasses. Later large quantities of waterfowl down and feathers are added. In several nests, pieces of white tissue (Kleenex) and also shredded cigarette filters were found.

Some of the nest cavities and tunnels were so thin that the walls of one burrow or nest would cave into

another when being examined. Two cavities that caved in were measured. One of these cavities was built directly over another with approximately 4 cm separation. It caved in quite easily when the nest was being dug out. A second had a side wall of only 3 cm between nests. Birds in these nests must surely be able to hear their neighbors.

The nests examined early in the period of egg laying contained very few feathers or down. Down was added during the incubation period. Bent (1942), Hoogland and Sherman (1976), Johnson (1958), and Petersen (1955) all found that feathers were usually added after laying of the last egg and during the incubation period. Petersen (1955) indicated that ". . . probably the presence of eggs in the nest is an external condition necessary for seeking and carrying feathers to the nest." I found feathers added after the first egg and prior to laying of the last egg in 8% of the nests. In 2% of the nests, feathers were added before laying of the first egg.

Fights over feathers were observed on five occasions in three separate colonies. In each case, a bird returning with a feather was "mobbed" by the other birds in the colony. They were all evidentally trying to get the feather. In the melee the feather was dropped several times, but immediately picked up by another bird. These feather fights were observed by Beyer (1938), Hoogland and Sherman (1976), and Petersen (1955). Publications by

Hoogland and Sherman (1976) and Petersen (1955) related observing birds stealing feathers from neighbors' nests. However, they stated that such robberies occurred too infrequently to permit intercolonial comparisons.

Mating

Sexual flights many times ended in copulation by the pair. Bent (1942) says that:

> One may see a pair of swallows emerge from the nesting holes and tussle with each other in the air, sometimes falling together to the base of the nesting bank and there apparently going through the act of copulation.

Stoner (1936a) also states that "Several individuals may congregate in a particular part of a sand pit or on a given section of a creek bank, with much chattering and fluttering and occasional mating." This type of behavior, however, was not observed. Shortt (1977) related that because "almost every activity of swallows is performed on the wing, early writers claimed that they even mate while in flight (not true!)."

Petersen (1955) reports some very interesting and apparently promiscuous copulations. On two different occasions he observed dead swallows lying at the foot of the bank being mounted repeatedly by several birds in quick succession in apparent attempted copulation. He states that "In one instance this gave rise to an orgy of mountings both of the dead bird and of other copulating

birds." He also placed a stuffed and mounted bank swallow skin on the ground, and this elicited the same reactions as the dead birds. However, he was unable to find any evidence of semen emission on the dummy.

I observed very few actual copulations. It seems likely, especially with the large number of birds studied and the absence of observations, that copulation usually takes place in the nesting chamber as Emlen (1954) described in the cliff swallow (Petrochelidon pyrrhobota).

Eggs and Clutches

Bank swallows generally lay one egg per day until the clutch size is reached. The one egg per day laying rate was observed in this study, and Petersen (1955) and Stoner (1936b) reported the same rate. According to Hoogland and Sherman (1976) the one egg per day laying pattern has also been observed in barn swallows (Hirundo rustica), cliff swallows, purple martins (Progne subis), and tree swallows (Iridoprocne bicolor).

All bank swallow eggs observed were pure white as described by Reed (1965) and Forbush and May (1955). However, Palmer and Fowler (1975) and Forbush (1929) stated that they may be white with a rosy tinge. Eggs, from 30 sampled, averaged 1.8 x 1.3 cm with a range of 1.5 to 2 x 1 to 1.4 cm, and weighed approximately 5.67 grams.

In 1977, 22 nests were examined containing eggs resulting in a mean clutch size of 4.45 ± .80 eggs. However, examination of 220 nests in 1978 resulted in a mean of 4.05 ± .78 eggs (Table 7). Petersen (1955) found an average clutch of 4.8 eggs from 125 nests, and Hoogland and Sherman (1976) reported an average clutch of 4.98 ± 0.05 from 217 nests (Table 8).

Table 7. Frequency of clutch sizes in nests located on Eielson AFB.

		Clutch Size					
	Clutch	2	3	4	5	6	Mean ± S.D.
1977	Frequency	0	2	10	8	2	4.45 ± .80
1978	Frequency	12	24	126	57	1	4.05 ± .78
*Total	Frequency	12	26	136	65	3	4.09 ± .78

* Paired t-test at .01 level of significance indicates no difference between 1977 and 1978 clutch sizes.

Table 8. Reported clutch size in the bank swallow.

Authority	Locality	Clutch Size
Lack, D. (1947)	England	4-5
Lack, D. (1947)	Central Europe (Saxony)	5 (6)
Lack, D. (1947)	Eastern Galicia	5-6
Lack, D. (1947)	Norway	(4) 5 (6)
Forbush (1929)	New England States	3-7
Witherby, et al. (1940)	Great Britain	Usually 4-5 Sometimes 3,6, or 7
Niethammer (1937) (Cited in Petersen, 1955)	Germany	5 (4-7)
Stoner (1936b)	New York State	Early Broods: 4 or 5 Late Broods: 3 or 4
Stoner (1936b)	Iowa	5 or 6 eggs (4 or 5 young)
Cory (1909)	Illinois and Wisconsin	3-6
Petersen (1955)	Dane County, Wisconsin	Before June 15: 5.0 After June 15: 4.0 Entire Season: 4.8
Hoogland and Sherman (1976)	Ann Arbor, Michigan	4.98±0.05
Reed (1965)		4 to 6
Palmer and Fowler (1975)		3 to 7
Lack (1948) size for Hirundinidae	Mid-Europe	5.0
	Tropical	2.7
This Study	Eielson AFB, Alaska	4.09 ± .78

Lack (1948, 1954) believed that the clutch size in passerine birds is related to the number of young birds that can be successfully reared without underfeeding due to division of food among many young. This is further indicated by Klopfer (1962) who stated that ". . . as the number of eggs in a clutch increased, the probability that the young would survive decreased." In fact, there is an optimum clutch size where probability of survival decreases when the size is increased. However, if it is decreased, survival is increased but it represents a smaller future population. Lack (1948, 1954) stated that there is an increase in clutch size with latitude. This is due, he believed, to the denser food supplies and longer length of daylight. However, no such real correlation could be drawn by comparison of clutch sizes in this study to those in southern areas (Table 8).

The fact that longer lengths of daylight provide greater periods for foraging are important. Swallows in Alaska are nesting and rearing young for a shorter period of time than those birds further south. For Alaskan birds, the length of migration is much longer than for southern individuals, thus requiring greater energy reserves. Consequently, both young and adult birds must reach peak condition, for longer southerly migrations, in a more compressed period than southern swallows. Their reserves would at least have to hold them until they could make

refueling stops in warmer zones. Thus clutches may only increase with latitude to a point. They then will pass the optimal level for maximum survival.

Incubation

Incubation of the eggs was not directly observed. Furthermore, sexes of the individuals entering and leaving the burrow could not be determined, unless the birds were captured. However, Stoner (1936b) was able to determine, through dissection, that both sexes do incubate the eggs. Stoner also determined that it was 14 to 16 days counting from the date on which the last egg was laid to that of the first hatching. However, Burns (1915) lists the incubation period as 12 or 13 days. Petersen (1955) states that ". . . the incubation period under natural conditions was found to be 15 days." In my study 14 and 15 days of incubation were required.

It was noted that incubation began before laying of the last egg. Petersen (1955) found, when examining the embryos, a difference of two to three days in age of greatest and least development. He relates that the difference in age of embryos is not tied to clutch size, but incubation begins with the laying of the third, fourth, or fifth egg. However, it may be as Purchon (1948) noted in the barn swallow (Hirundo rustica) that eggs are incubated each day for a short time. This activity is increased

each day until full incubation is reached. Differences found in times of hatching and sizes of young verify unequal incubation of eggs.

Viewing Pit

So that direct observations could be made of nest activities, a viewing pit was made at one burrow, as described in the methods section. The pit was constructed on the evening of 4 June 1978 at the colony across from the Top of World Sportsman's Association (TOWSA). The nest cavity contained grass but no eggs at this time. On 5 June the nest had more grass added to it, and a layer of condensation had collected on the glass. On 6 June one egg was found in the nest and considerable condensation was still present on the glass. On 7 June there was still only one egg, but the condensation was gone. The pit was not checked on 8 June, but on 9 June there was fresh soil completely covering the nest. The birds had started digging the burrow deeper. The old nest and egg were completely covered over. On 10 June a new nest cavity with grass was found 25 cm back from the old nest. On 11 June the new nest contained one egg. Eventually four eggs were laid in the new nest.

Why the swallows abandoned the nest at the pit is not known. Perhaps it was the disturbances at the pit. Perhaps some light was leaking in through the viewing glass,

or perhaps it was the condensation on the glass. The condensate on the glass was from either evaporation of soil moisture, expiration from the birds or both. The birds were occasionally in contact with the glass, consequently they would get wet. In the future, I believe the glass should be tilted to drain off condensate. Also, an additional tarp should be placed over the trapdoor at the surface, to eliminate the possibility of any light leakage.

Egg Recognition and Losses

During 1978, several eggs were found in tunnels, at burrow entrances and on the ground below colonies. This was not observed in 1977. On 10 June 1978, at the Quarry Road colony, two eggs were found at the lip of one burrow entrance and another on the ground below the colony. On 11 June 1978, one whole egg and two broken eggs were found on the ground. On 12 June 1978, two more eggs were found in another tunnel between the nest and the entrance. On 13 June 1978, one whole egg and four broken eggs were found on the ground. Again on 18 June 1978, one broken egg was on the ground and three were grouped together out of the nest in one burrow. One explanation is that the birds in their haste to leave the nests were knocking the eggs out. There is also the possibility of (a) mass disturbance(s) that would have flushed many birds from the nests. Probing had been carried out in all of these holes

with the light and mirror every day. Consequently, there was disturbance every day. However, this was also done at the other colonies, and only one egg was ever found on the ground at other colonies. There was no evidence of a predator moving the eggs. No reference to this phenomenon could be found in the literature.

When digging up nests for examination in 1977, eight eggs were transferred to other nests. Two eggs were placed in each of four different nests using a plastic spoon tied to a stick. The nests were in nearby burrows of the same colony. It could not be positively determined if all of the nearby nests contained eggs, with the exception of one nest where the eggs could be seen. Later, two of the nests produced six and seven young, indicating that the eggs may have survived the transfer. In 1978, this experiment was repeated by marking and transferring eggs from each of six nests into six other nests. All six of the transferred eggs were accepted and hatched by the receiving birds. Two other eggs were accidentally broken, each in separate nests, with my mirror. In each case, the eggs were removed by the birds.

Hoogland and Sherman (1976) relate that bank swallows are unable to recognize their own eggs. In their study, they took nine marked eggs from two nests and placed them singly in each of nine other nests. All of the receiving nests already had eggs. None of the eggs were rejected

and eight of the nine eggs hatched. The ninth egg was in a nest which was abandoned. When they later cracked six eggs, these were rejected by the adult birds. This indicates that the birds were able to identify and reject defective eggs.

Eggshells were removed from the nest upon hatching. Two birds were observed removing shells. Eggshells were seldom found anywhere around the colony, and few birds were seen removing shells, indicating that they may eat them.

Brooding

It was found that the young were brooded almost constantly for the first few days after hatching and for decreasing periods thereafter. Beyer (1938) believes that this continuous early brooding is apparently done only by the female, while the male parent forages for food. However, Stoner (1936b) ascertained, through dissection, that both sexes brood the young. However, he did not mention whether or not the female was the primary brooder during the first few days.

Feeding

Activities around the burrow entrances increased noticeably after the hatching of young. The parents made frequent trips to collect food and feed the young. From

careful observation it was apparent that both of the parents feed the young. This was suggested by frequent visits of adult birds to the burrow and the occasional occurrence of two birds arriving at the same time. During the rearing period, 9 adult birds in 1977 and 35 in 1978 were marked and observed. At no time was a marked bird seen to enter any burrow but its own. Nor were marked birds observed or recaptured at any colony other than their own.

No observations were made of food being carried to the young. This is probably because of the large number of smaller insects being eaten. In addition, the closed nature of the nests precluded further observations. Stoner (1928) captured an incubating bird which carried in its bill a crushed two-winged fly (Diptera) and a small cicadellid (Homoptera). Beyer (1938) observed that in the first few days the young were fed mostly small soft-bodied insects (Diptera). Later, mayflies were the main article of food. According to Martin, et al. (1961) and Stoner (1936b), all species of swallows capture practically all of their food on the wing. In addition, Beal (1918) reported that, "the insects eaten most commonly are beetles of various sorts (including weevils, May beetles, and ground beetles), winged ants, wasps, bees, flies, bugs, moths, and dragonflies." Furthermore, Beal (1918) found in the examination of 394 stomachs of bank swallows col-

lected in 21 states and Canada that 17.9% of the food consisted of Coleoptera. Ants, chiefly winged forms, composed an additional 13.39% of food in the stomachs. Ants were found in 121 stomachs and formed the total contents of 11 stomachs. Various other species of Hymenoptera were found in 207 stomachs. The Hemiptera comprised nearly 8%, Diptera 26.63%, Lepidoptera 1.21%, Odonata 2.11%, and other miscellaneous insects eaten comprised 10.53% of the food. A few spiders were included in the stomach contents of swallows studied by Beyer (1938). Bent (1942) said, "the food of the young is similar to that of adults, but that of the younger nestlings contained an excess of soft-bodied forms of insects."

Palmer and Fowler (1975) reported that the foods are essentially insects, with an obvious emphasis of flies and weevils. They do, however, make one other interesting comment:

> Cold rains, which keep flying insects down during the time young are developing, are often fatal to great numbers of swallows and swifts. If food is not in air, birds do not get it.

This is further verified by Griffin (1974) and Hoogland and Sherman (1976). In June 1977, there were many cold rains in the Eielson area, however, most young birds were not hatched until late June. It would be interesting to compare the survival rate of the young from dry and wet years. However, data of this type was not recorded.

Bank swallows are social foragers. When one bird finds food, the fact is somehow communicated to others. Soon there is a steady stream of birds flying between the colony and the feeding area. With many individuals searching for food, foraging efficiency is greatly increased. This is especially critical for the young to be fit for the southward migration. Emlen and Demong (1975) stated:

> Since a fledgling's initial foraging attempts are bound to be somewhat inefficient, it can benefit greatly by parasitizing information from other colony members and thus minimizing the time and energy spent in finding and traveling to suitable feeding areas.

The longer periods of daylight permit prolonging the daily feeding process by several hours. Consequently, the nestling phase may be speeded up over that of birds further south (Griffin 1974).

The frequencies of visits to the burrows, supposedly for feeding and nest sanitation, were recorded. During 1977, it was found that the shortest time between visits was 25 seconds and the longest 17 minutes. An average taken from 597 visits to two nests, showed that the average time between visits was four minutes 36 seconds over a composite 17-hour period, or an hourly rate of 22.1 visits per hour (Table 9). This 17-hour period was a composite developed from 0500 to 2200 hours over eight days. During peak periods, the visits averaged one every 80 seconds. The peak period of feeding in the study was from approxi-

mately 1800 hours to 2000 hours. Observations were made during the same week each year and in this instance, during the same phase of the nesting cycle.

Table 9. Mean hourly feeding rate for nestlings as reported by Petersen (1955) and noted during this study.

Source of Data	Locality	Hours of Observation	Feeding Rate
Petersen (1955)	Wisconsin	33	24.7
Beyer (1938)	Ohio	2	24
Moreau and Moreau (1939)	England	24	33.3
Stoner and Stoner (1941)	New York	56	17.1
This Study 1977	Alaska	17	22.1
This Study 1978	Alaska	12	28.2

In 1978, the frequencies of visits were measured for 12 hours of composite observation over six days. Six to eight nests were observed simultaneously in 15 to 30 minute blocks. There were 794 visits to 44 nests recorded in three colonies over a 14.5 hour period, from 0600 to 2030 hours during six days. The time between visits ranged from 3 seconds to 17 minutes and 5 seconds with a mean feeding rate of 28.2 times per hour.

A daily average number of feedings may differ if more nests are studied over a more extensive period of time. Petersen (1955) observed the hourly feeding rate to be 24.7 per hour for 33 hours of observation. Beyer (1938)

found at the one nest he observed for 15 hours, that food was brought 115 times with the length of time between feedings ranging from one to 15 minutes, averaging less than 5 minutes. It was noted that as the young became older they are fed at the burrow entrance, making observation much easier. It was also observed at this time that usually only one nestling is fed at a visit. Young birds were frequently seen "begging" from parents of nearby burrows. However, they were never observed to be fed by other than their parents.

Nest Sanitation

Nest sanitation was maintained up to the period just after the fledging of the young. The adult birds were observed regularly removing fecal pellets. In many instances, the pellets were dropped close to the burrow. Beyer (1938), making observations of birds in the nest cavity, observed the parent birds swallowing the fecal pellets during the first five or six days, and then carrying them outside the remainder of the time. Stoner (1936b) made the following observations:

> The young usually deposit the pellets on the edge of the nest, and seldom in it. With young approximately seven to 12 days old, the pellets are often deposited in a little group a few inches from the nest. By aid of a beam of light, young were observed to crawl out of the nest to defecate, and then to shuffle back again. Returning parents begin at once to remove the pellets, and keep at the task until it is finished.

These piles of fecal pellets were observed near the nests in several burrows. At about two weeks of age, the young begin to appear regularly at the burrow entrance to be fed and occasionally to void fecal pellets there. Fecal pellets and droppings cover the ground immediately in front of the colonies. However, the burrows and entrances remain relatively clean. I did find a burrow that was completely covered at and below its entrance with droppings. This was in direct contrast with the remaining burrows in this and other colonies.

Removal of fecal pellets was recorded during the observations of feeding rates. From those that were observed, fecal pellets were removed approximately every 13.1 visits.

Recognition of Young

One evening I dug up a nest of four young birds for examination. The birds were approximately five or six days old, using Beyer's (1938) plumage criteria for age determination. Two of these birds were placed in each of two nearby nests which also contained young birds. Petersen (1955), from observations of individually marked parents, stated that,

> Bank swallows can distinguish their own nestlings from others, and will feed only their own nestlings, even when they have left their own burrow and returned to the same or another burrow.

In one nest of transfers, it appeared that the parent birds had abandoned the nest. This was two days after the transfer; and no movement was seen in the nest cavity. Upon digging up the nest, seven dead young were found. In the second nest, six young birds were raised. Presumably with average clutches between four and five, one or even two of these birds were those transferred to the nest. No dead young were ever found at the base of the hill below the burrow or in the nest itself. Perhaps there is a point at which the parents begin to recognize their own young and will no longer care for the young. In future studies, perhaps more transfers of young should be tried. The one nest could also have been abandoned due to the excessive disturbances in the area, or any number of other variables.

Young

When young were dug up at five days of age, the birds crouched in the back of the chamber when a shadow covered the hole. When the young birds were placed in new burrows, they immediately began shuffling down the tunnel to the nest chamber. Beyer (1938) also observed that, ". . . when returned to the entrance of the burrow the young run eagerly back into its dark interior." Bent (1942) found that young birds eight to 15 days old have a tendency to shuffle backwards when placed on the ground outside the

burrow; but this also manifested itself before they left the burrow.

After the young birds are partly grown, and no longer require brooding, the adults leave the young alone in the burrows at night. Arriving at one colony at 2245 hours on 6 July 1977, it was obvious that there were no birds flying or in evidence anywhere. This colony was located 125 meters southeast of Engineer Hill on Eielson Air Force Base. While investigating the burrows, an adult bird flew over the colony and then flew back to the southwest toward Lily Lake. Within a few minutes, many birds were circling overhead and entering the burrows as usual. Evidently, all the birds had been roosting somewhere near the lake approximately 300 meters away. Later, at a colony located at Central and Division Avenue on Eielson AFB, adult birds were observed roosting on power lines 150 meters from the colony. These adult birds were from the nearby colony. Adult birds were also missing from other colonies I checked. I was able to find the roosting place of my largest colony. The roost was located on power lines approximately 400 meters southwest of the colony (Figure 7). This roost was used both years by this colony. Stoner (1926) found, that when the young were fairly well developed, ". . . it was somewhat of a surprise to find that the adults were so uniformly conspicuous by their absence." Petersen (1955) found that the parents were rarely found

at night in the burrows containing nestlings over 12 days old.

At nine to ten days old, the young could be found out of the nests and in the tunnels. Within another several days, the young begin appearing at the burrow entrance. At first they wait just back from the entrance for the adult birds, but they soon crowd in the opening when a parent appears. At this time, the young are being fed at the entrance and in the tunnel.

As the young begin to fledge, they spend most of their time at the burrow entrance. It is not unusual to see three or four young all crowded together at the entrance. At fledging, many of the young were observed making their first flights. Usually these flights were erratic and of short duration. During these early flights, the young birds tired easily. In one instance, the young bird hit the ground in front of the burrow, being unable to keep himself airborne. These early flights from colonies over water are known to take a toll of several of the young, and one bird was observed to descend into the water.

Actually, the young birds fly well on the first flight. This is remarkable since they have been confined to a burrow and cannot exercise their wings. Stoner (1926) states that,

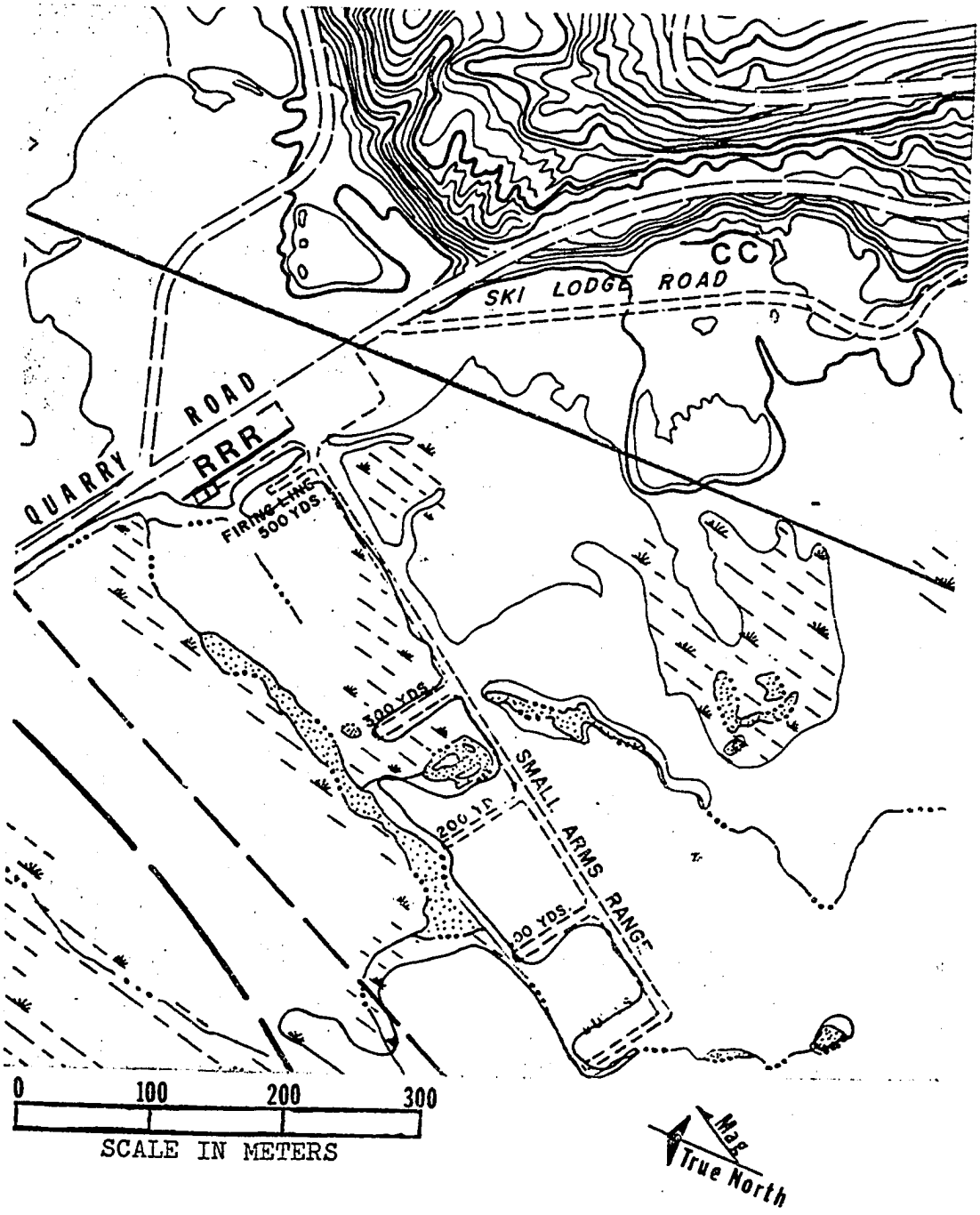


FIGURE 7. Map of the Quarry Rd. colony off of Ski Lodge Road, Eielson AFB. CC marks the colony on the map, and RRR marks the roost.

> While the young appear to be a little more uncertain of their equilibrium in the air and flap their wings rather more rapidly than the adult, they seem to acquire the ability of the parent in a few seconds and dart and zig-zag in remarkable fashion.

The ability to fly seems to be inherited and their performance improves during the bird's life. Maturation of this behavior develops with the age of the individual. Burton and Burton (1977) state that sand martins' and puffins' ". . . ability to fly appears when the bird has reached a certain stage in its development and practice is needed only for the fine control of flight."

At about the time the young birds fledged, several were caught and marked. In 1977, 30 birds were marked and an additional 49 in 1978. Many of these were the young of previously marked adults. These marked birds were from three different colonies. This was done to aid in determining the movements of the young birds at the time they were first flying. It was done to see if they could differentiate their burrows from others on their return flights and also to determine if any mixing of the young occurred in the burrows.

Young birds could usually find their home burrows and did return to them, at least during the first few days after fledging. However, some marked birds were seen flying to burrows other than their own. They usually did not remain long and may only have been investigating other

burrows. One factor that may help the young return to their home burrows is the calling of their nestmates. Usually all the young will be crowded around the entrance and all are calling constantly. The young bird may not initially recognize the burrow at all but may only be returning to its nestmates. In the first few days, the only burrows, other than home burrows, the marked birds spent time in were nonactive burrows. The young birds would also congregate on the edge of the bluffs over the colony. Marked young were observed roosting with the adults just prior to migration.

One interesting thing discovered was that after a few days, the young do not always return to the home burrow. Young birds were frequently recorded entering burrows other than their own. In addition, marked birds captured in the burrows were not always from that burrow. Twenty-eight previously marked young birds were captured at the burrows when almost all birds had been fledged for several days. Of these, five, or 17%, were not in the home burrow.

Young birds tended to congregate on nearby utility lines and at the colony site. It was not unusual to see six birds sitting under or on a dirt ledge at the colony. Within several days most young leave the burrows, foraging further from the colony and roosting together or with the adults.

Predation

Evidence of predation was discovered in two of the study colonies during 1977. Both colonies were located in heavily wooded areas. Signs of predation included scratch or claw marks and digging at the burrow entrances. Early in the spring, while making burrow measurements, the remains of a bird from the previous year were found. The entrance to the burrow had claw marks and the bird's left wing was found just inside the burrow. It could not be determined conclusively what predator was small enough to enter the burrows without digging. However, the red squirrel (Tamiasciurus hudsonicus), least weasel (Mustela rixosa), and shorttail weasel (Mustela erminea) are prime candidates, due to their abundance in the area. In each case the depredated nest was a lower peripheral nest in the colony.

The only possible predators that were seen near any of the colonies were a cat (Felis domestica), ravens (Corvus corax), American kestrels (Falco sparverius), hawk owl (Surnia ulula), mew gull (Larus canus), and red squirrels. A list of possible mammalian predators is in Table 10.

Table 10. List of possible mammalian predators on bank swallows.

Red Squirrel - *Tamiasciurus hudsonicus*
Black Bear - *Ursus americanus*
Marten - *Martes americana*
Shorttail Weasel - *Mustela erminea*
Least Weasel - *Mustela rixosa*
Wolverine - *Gulo luscus*
[1]River Otter - *Lutra canadensis*
[1]Mink - *Mustela vison*
Lynx - *Lynx canadensis*
Red Fox - *Vulpes fulva*
Coyote - *Canis latrans*
Wolf - *Canis lupus*
[1]Not known near area of study

Where they occur, the red squirrel is possibly one of the primary mammalian predators. Red squirrels were common at both the colonies where predation occurred and they are suspects in the predation. Palmer and Fowler (1975) state that, "The red squirrel may eat possibly 200 birds a season and therefore be worse than a domestic cat." Furthermore, Martin, et al. (1961) report that "The red squirrel seems to have a strong predilection for flesh. It eats insects, young birds, and eggs." Further indica-

tions of the red squirrel's taste for birds and eggs were found in papers by Hamilton (1939) and Hatt (1929).

Potter (1924) discovered an area on a cliff where a badger (Taxidea taxus) dug down into bank swallow nests and ate the birds. Errington (1932) reported bank swallows preyed upon by a barred owl (Strix varia), and Stoner (1938) reported a crow (Corvus branchyrhynchos) eating swallows. Stoner further related that adult bank swallows were killed and partly eaten in their burrows by house rats (Rattus norvegicus). He also recorded finding a deer mouse (Peromyscus leucopus), a common flicker (Colaptes auratus), a western harvest mouse (Reithrodontomys megalotis), and various insects in the nesting burrows of bank swallows. In addition, Ginevan (1971) reported eastern chipmunks (Tamias striatus) entering burrows and killing adult bank swallows. Morlan (1972) observed a northern strike (Lanius excubitor) preying on a swallow in a mist net and brown bears (Ursus arctos) digging up a swallow colony. However, studies show that the swallow's nesting burrows provide protection from most predators. Windsor and Emlen (1975) reported on observations of over 500 nests indicating that losses of eggs or nestlings amounts to less than 13% of the total eggs laid.

Bent (1942) and Brewster (1903) related a case where a mink destroyed a colony of bank swallows. There were 108 holes, but all except one pair were killed by the mink.

In another colony, 22 nests located along the bank of a river were reported to have been destroyed by either a mink or weasel.

The bank swallows would be most vulnerable to predation at the time the young are fledging. This is verified by Windsor and Emlen (1975) who observed that most predation by kestrels occurred when many colonies had broods near to or actually fledging. At this time young birds are at the entrance of the burrows and they are very vocal, thus attracting predators. In fact, young birds will even come to the burrow entrance when any motion is detected. This is probably in response to what they believe to be the return of the parent birds. At the time of fledging, it is also easy to get the young birds to fly from the nest. However, an adult bird will usually stay back in the burrow when approached, and is much more difficult to get out.

Tinbergen (1946) cited numerous examples of how the activity and habits of a bird increase the risk it runs of being preyed upon by the Old World sparrow hawk. Tinbergen pointed out that noisiness and gregarious habits tend to increase the vulnerability. Craighead and Craighead (1969) state that:

> Movement and activity increase the conspicuousness of a prey species, which in turn usually increases its vulnerability to predation. It is safe to state that, in general, a total prey population shows greater activity and movement

> during the reproductive season, and in this respect, then runs a greater risk from captors than at any other time.

Craighead and Craighead (1940) state that, "Swallows are invulnerable to most North American raptors except the Pigeon Hawk (Falco columbarius)." However, Freer (1973) documented that American kestrels do attack swallows both in flight and at their burrows. Freer's observations were supported by observations made by Windsor and Emlen (1975). Kestrels were observed at colonies, watched during this study, three times in 1977 and five times in 1978. In one incident, a kestrel caught a young swallow at the burrow. A kestrel also attempted to take a swallow caught in a mist net. However, it was frightened away by banding personnel. In every instance, the kestrels were mobbed by swallows when they approached the colony. However, in one instance the kestrel landed at the edge of the colony and mobbing ceased until it flew again.

In 1978, an interesting incident was observed of cliff swallow predation by mew gulls. The incident took place at a large cliff swallow colony one-half mile from one of my study colonies. Several hundred cliff swallows were flying and feeding in front of the colony when two gulls appeared. The gulls immediately singled out a swallow and began rapid aerial pursuit. The other swallows began mobbing the gulls. The gulls seemed to ignore the harassment and continued pursuit. The pursuit contin-

ued for several minutes at high speed and involved intricate maneuvers. The gulls struck the swallow, and it fell to the ground. One gull then began to feed on the bird. Mew gulls are common in the area and they should be considered potential swallow predators.

One colony, located along Jack Warren Road on the way to Clearwater Campground, mile 95.6 on the Richardson Highway southeast of Fairbanks, was completely destroyed by predator(s). There were approximately 50 burrows in this colony and almost every hole was dug out from its entrance. No birds were observed at this colony. This colony was built along a dirt shelf only about a meter high. This made it extremely vulnerable to predators.

There was no evidence as to what type of predator may have dug up the colony. The length of time that the colony had been destroyed could not be determined. Claw marks on the sides of burrows were 5 to 8 cm apart. None of the burrows were dug back to the nest chamber. Most were only dug back 30 cm. This was seemingly sufficient to cause the resident birds to attempt escape. There are several humans habitations near this colony and it is very possible that dogs or cats may have dug up the colony.

Mobbing

In 1977, a cat was observed on three occasions at one streamside colony. The first time the cat was observed I

did not see it until I noticed the swallows mobbing. The birds circled the cat horizontally in several layers. Individual birds momentarily dipped and hovered in front of the cat. This was done with considerable vocal commotion. At no time was physical contact observed with the cat. The cat was not seen capturing swallows but its frequent visits to the area suggest that it had been successful.

A type of group defense behavior is demonstrated in mobbing reactions of bank swallows toward potential predators. "In addition to being bothersome, the advantage seems to be that the detected predator is unable to surprise a prey" (Eibl-Eibesfeldt 1975). The solitary nesting swallows such as the tree swallow (Iridoprocne bicolor) are the most aggressive and successful mobbers according to Kuerzi (1941) and Chapman (1955).

> In fact, the bank swallow, cliff swallow and house martin are reported to be even less aggressive and less effective in mobbing predators and nest-site competitors (Windsor and Emlen 1975, Emlen 1952, 1954, Lind 1962, 1964, respectively) (Snapp 1976).

Mobbing by bank swallows is an example of sympathetic induction as described by Tinbergen (1965). This behavior is initiated by an alarm note given by one member of the group which simply releases the behavior in the other birds (Armstrong 1965 and Thorpe 1956). In addition, young birds retreat into the burrow when they hear the

alarm note. Consequently, the alarm cries during mobbing serve as a warning.

Bank swallow mobbing was tested several times soon after burrows were completed. Reactions to the test mammalian predator began when a small dog was within 25 to 30 meters of the colony. The intensity of the mobbing decreased after the dog was present at the colony for greater than five minutes. The mammalian predator test was made during the excavation/nest building phase, the egg laying/brooding period and after most young were approximately six days old. The merlin model was tested during egg laying, incubation, when young were six days of age, and 15 days old, and again when most young were just fledged. In all cases, for both the mammalian and avian predator, mobbing took place.

One notable difference in the reaction to the avian predator was the distance at which it elicited mobbing. When the model was 15 meters from the colony no active mobbing took place. The swallows, however, concentrated at the colony and were much more vocal. However, they did not approach the model, although it was obvious that they were aware of it. When the model was moved to within eight meters, the reaction was about the same, but with an occasional bird flying near the model. However, there was still no actual mobbing of the model. To elicit real mobbing, the model had to be at or within 1.5 meters of the

colony and moving. In one instance, a kestrel landed at the edge of the colony and mobbing ceased until it flew again.

The difference between the two tests may have been the movement of the "predators." The dog was active and moving whereas the suspended model merlin was relatively motionless. It was noted that when the wind blew the merlin, the swallows increased their activity. To further test this, the model was flown in on a wire. In this case, swallows began mobbing at about 15 meters. In all cases, the model was headed straight toward the colony. Windsor and Emlen (1975) state that:

> A kestrel elicited alarm notes and organized group flying only when it was moving, particularly in flight. Shortly after it landed, regardless of its location within the colony, the alarm faded and birds resumed their normal behaviors. Nestling swallows returned when a kestrel perched nearby would have been in direct view.

At one colony of 204 active burrows, there were approximately 30 other burrows scattered randomly along approximately 100 meters of bank. These birds fed, mixed and were completely autonomous with the main colony, but were considered as separate nesters or subcolonies of the main colony. Approximately 30 adult birds from the "main colony" had been color marked. The model merlin was placed at the furthermost burrow of the subcolonists. Mobbing commenced more slowly with a relatively small initial num-

ber of birds. Presumably, these were resident adults from burrows near the model. Eventually, more and more birds joined the mob, including several color marked birds, verifying that members of the main colony were participating. However, a mob as large as the mob participating at the main colony did not gather at this peripheral site. Several birds moved back and forth between the "mob" and the main colony. Presumably they were staying close to their own burrows, but still participated, if only loosely, in the mobbing.

Formation of mobs and initial responses of birds was much slower at these peripheral burrows, and the mobs were never as large as those at the main colony. This is undoubtedly due to several factors. Individual parents were most concerned with their own burrows but did participate in mobbing at distant burrows. Mobbing behavior is more related to defense of burrow than it is to anti-predator behavior (Windsor and Emlen, 1975). Mob participation is stimulated by the calls and movements of other birds which released the appropriate rallying behavior in the other swallows. Mobbing is a sympathetic activity as described by Armstrong (1965) and Tinbergen (1965). Individual birds are concerned primarily with their burrows and the area immediately around them. Consequently, there are fewer birds watching the area around peripheral nests, thus delaying the initial alarm response.

My observations confirm the conclusion of Hoogland and Sherman (1976) based on observation of color marked birds

> (1) only adult birds mob, (2) individual parents mob predators that are attacking burrows very distant from their own, and (3) the mobbing response is usually initiated by one or more adults whose burrows are in the immediate vicinity of the predator's approach.

It was noted, as reported by Hoogland and Sherman (1976), that mobbing of predators occurred at all stages of the breeding cycle. However, birds did not actively mob prior to burrow selection. At no time were humans actively mobbed by more than a few birds, and this mobbing lacked the intensity of that of the mobs on models or predators.

Hoogland and Sherman (1976) observed:

> . . . several successful deterrences of Sparrow Hawks by Bank Swallow mobs under natural conditions. At Bank Swallow colonies near Ithaca, New York, D. Windsor and S. Emlen (personal communication) observed numerous attempts by Sparrow Hawks to capture adults and young, and they suggested that mobbing Bank Swallows 'seem to be almost totally ignored' by attacking Sparrow Hawks. However, D. Windsor and S. Emlen (personal communication) also observed that 16 of 25 attempted predations by Sparrow Hawks (64%) were unsuccessful. Perhaps some of the 16 failures resulted at least in part from Bank Swallow mobbing.

Windsor and Emlen (1975) stated that they were "struck by the utter ineffectiveness of the mobbing behavior of these swallows in deterring Kestrels." They indicated that mobbing may be as much a warning to the young as it is a means to drive away or harass aerial predators. They tested this

by observing the response of young birds to recorded alarm notes. They found that 67% of the young retreated during playback of the alarm note. In all tests alarm notes were releasers of retreat behavior in the young.

Late Breeding

Several instances of late migrants were recorded in 1978. On 18 August, I observed a pair of bank swallows feeding over Mullins Pit. They then returned to the colony located at the water's edge. I had assumed that this colony was abandoned on 6 August when I had last seen birds there. However, this lone pair was still present, and they had three young ready to fledge in a burrow which had contained another brood earlier. Evidently, this was a late or second brood.

In 1978, while on a kayak trip down Clearwater Creek near Delta Junction, Alaska, a pair of bank swallows were observed. They were feeding over the creek somewhere between Clearwater Campground and Clearwater Lake. It was 31 September and quite cool that day. However, they were feeding on an insect hatch above the warm water of the creek. That night was below freezing, and the next day was cold with sleet and snow. I doubt that these birds would have made it south before being caught by cold weather. There was no colony site or other birds in evidence

at this location. It is unknown whether these were local birds or migrants.

According to Kessel and Gibson (1978), bank swallows are ". . . common to locally abundant breeders through central Alaska between mid to late May and mid-August." The latest recorded swallow around Fairbanks is 20 August. The latest swallows at my colonies were recorded on 7 August 1977 and as previously described on 18 August 1978. However, all other colonies were abandoned by 6 August in 1978.

Colony Sharing

In one large colony, located along the Edgerton Highway above the settlement of Lower Tonsina, at least six burrows were occupied by violet-green swallows (Tachycineta thalassina). There were approximately 100 burrows in the bank swallow colony. The violet-green swallow burrows were below and at the outer edge of the bank swallow burrows. The information from Pough (1957) and Peterson (1961) indicated that the violet-green swallow will use existing holes in cliffs. From this information, it is also assumed that the violet-green swallow will occupy abandoned bank swallow burrows. Coulson (1968) reported that there is more intense competition for nest sites in the center of a colony, and Petersen (1955) hypothesized that higher nests are preferred over lower

ones. Coulson (1968) showed, in kittiwakes (Rissa tridactyla), that the individuals on the edge of the colony had a 60% higher mortality rate, in the males, than those in the center. Perhaps this less intense competition for the burrows at the edge also occurs in bank swallows, consequently allowing the violet-green swallow to establish themselves at the lower edge of the bank swallow colony. Emlen (1971) reported that lower peripheral nests of bank swallow colonies are less successful than upper or central nests. He suggests that the differences were the result of increased abandonment of peripheral nests and Hoogland and Sherman (1976) suggest that it is differences in group defense.

CONCLUSION

Burrow sites do not appear to be limiting. The distribution of burrows within a colony site, where only a limited area is used, and the absence of isolated burrows, would indicate this. In addition, many seemingly suitable sites are unused or little used. The birds clump their burrows even when there is adequate space (Hoogland and Sherman 1976). However, it is difficult for human observers to determine what sites are suitable. Spencer (1963), in Hoogland and Sherman (1976), found that bank swallow colonies were not located in any particular soil type. He also suggested that clumping of burrows is not related to available suitable habitat.

If there were shortages of suitable habitat, then every suitable site should be fully used each season. However they were not, as both the colony abandonment and annual fluctuations in this study indicate. Bergstrom (1951) found that the number of swallows nesting at a specific site for seven years fluctuated considerably. This is also reported by Stoner (1926, 1936a) and Hoogland and Sherman (1976). Unfortunately, the tendency of bank swallows to readily occupy man-made sites makes them highly vulnerable to destruction. The chances of establishing colonies in less stable soils is greater at newly dis-

turbed sites. The colony runs a great risk of further man-caused disturbances and ultimate destruction of the colony. This is significant at northern latitudes, since chances for successful second nesting attempts are limited. If destruction takes place very early in the cycle, there may be time for renesting. However, the short length of the nesting season in the north reduces the likelihood of a successful second nesting.

Synchronization of activity is very obvious throughout the nesting season. Hickling (1959) says that "it must be the cumulative stimulation of the displays which synchronizes breeding condition throughout the colony." In every activity from sexual flights through burrow excavation, egg laying, feeding and final fledging of the young, a great intracolonial synchronization is evident. In all of these activities, the current behavioral activity appears as a communal effort, although each pair is concerned primarily with their burrow or young. These events appear as communal activities and could not be so without this synchronization. "The strongest effect is that laying, hatching, and fledging are almost simultaneous throughout the group or colony." (Hickling 1959).

This close synchronization places all birds in a colony in the same cycle. Consequently, the most vulnerable periods for predation, when young are more vocal or fledging, are greatly reduced within an individual col-

ony. Protection is further enhanced by the intracolonial cooperation and gregariousness of the birds evidenced in group mobbing of predators.

It is extremely difficult to determine the successes or failures of predators at bank swallow colonies. Many diurnal nonavian predators and most avian predators leave no evidence of predation attempts. Although mobbing is sometimes successful, it is difficult to measure. It seems that large bank swallow colonies would be more effective than smaller colonies in discouraging predators, because of the volume of mobbing birds.

I believe that a more extensive study of the bank swallow in interior Alaska would be worthwhile. More data are needed for phenology, production, breeding behavior, food habits, care of young, coloniality, and effects of predators. A more extensive banding program should be initiated to retrieve information on the mixing of birds between colonies, establishment of new colonies, other intercolonial comparisons, and returns of individuals to specific colony locations or even specific burrows.

There is an abundance of swallow colonies in interior Alaska and these would facilitate such studies. Preliminary study indicates that the nesting phenology of swallows in the interior may be different from that of swallows further south. Furthermore, little research has been conducted on the bank swallow in Alaska.

LITERATURE CITED

Armstrong, E. A. 1965. The ethology of bird display and bird behavior. Dover Publ., Inc., New York. 431 pp.

Beal, F. E. L. 1918. Food habits of the swallows, a family of valuable native birds. U.S. Dept. of Agr. Bull. 619:26-28.

Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Nat. Mus. Bull. 179:400-424.

Berger, A. J. 1961. Bird study. Dover Publ., Inc., New York. 389 pp.

Bergstrom, E. A. 1951. The South Windsor bank swallow colony. Bird-Banding 22:54-63.

Beyer, L. K. 1938. Nest life of the bank swallow. Wil. Bull. 50:122-137.

Brewster, W. 1903. A tragedy in nature. Birdlore 5:151-152.

Burns, F. L. 1915. Comparative periods of incubation of some North American birds. Wil. Bull., 27:275-286.

Burton, M. and R. Burton. 1977. Inside the animal world, an encyclopedia of animal behavior. The New York Times Book Co., Inc., New York. 316 pp.

Chapman, L. B. 1955. Studies of a tree swallow colony. Bird-Banding 26:45-70.

Cory, C. B. 1909. The birds of Illinois and Wisconsin. Fld. Mus. of Nat. Hist. Publ. 131:56-57.

Coulson, J. C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217:478-479.

Cox, R. A. F. 1961. Sand martins nesting in a heap of sawdust. Brit. Birds 54:205.

Craighead, J. J. and F. C. Craighead. 1940. Nesting pigeon hawks. Wil. Bull. 52:241-248.

_____. 1969. Hawks, owls and wildlife. Dover Publ., Inc., New York. 143 pp.

Eibl-Eibesfeldt, I. 1975. Ethology, the biology of behavior. Holt, Rinehart and Winston, Inc., New York. 625 pp.

Emlen, J. T. 1952. Social behavior in nesting cliff swallows. Condor 54:177-199.

_____. 1954. Territory, nest building, and pair formation in the cliff swallow. Auk 71:16-35.

Emlen, S. T. 1971. Adaptive aspects of coloniality in the bank swallow. Abstr. Am. Zool. 11:47.

_____. and N. J. Demong, 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. Science 188(4192):1029-1031.

Errington, P. L. 1932. Food habits of southern Wisconsin raptors. Condor 38:176-186.

Forbush, E. H. 1929. Birds of Massachusetts and other New England States. J. S. Cushing Co. Norwood, Mass. 3:158-161.

_____. and J. B. May. 1955. A natural history of American birds of eastern and central North America. Bramhall House, New York. 552 pp.

Freer, V. M. 1973. Sparrow hawk predation on bank swallows. Wil. Bull. 85(2):231-233.

Ginevan, M. E. 1971. Chipmunk predation on bank swallows. Wil. Bull. 83(1):102.

Greenlaw, J. S. 1972. The use of sawdust piles by nesting bank swallows. Wil. Bull. 84(4):494-496.

Griffin, D. R. 1974. Bird migration. Dover Publ., Inc., New York. 180 pp.

Hamilton, W. D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31:295-311.

Hamilton, W. J., Jr. 1939. Observations on the life history of the red squirrel in New York. Amer. Mid. Nat. 22(3):13.

Hatt, R. T. 1929. The red squirrel: its life history and habits. Roos. Wldl. Ann., N.Y. State Col. 2(1):143.

Hickling, R. A. O. 1959. The burrow-excavation phase in the breeding cycle of the sand martin Riparia riparia. Ibis 101:497-500.

Hoogland, J. L. and P. W. Sherman. 1976. Advantages and disadvantages of bank swallow (Riparia riparia) coloniality. Ecol. Mono. 46:33-58.

Johnson, O. W. 1958. Observations on a colony of bank swallows near East Lansing, Michigan. Jack-Pine Warbler 36:173-177.

Kessel, B. and D. D. Gibson. 1978. Status and distribution of Alaskan birds. Coop. Orn. Soc. Studies in Avian Biology #1. 100 pp.

Klopfer, P. H. 1962. Behavioral aspects of ecology. Prentice-Hall, Inc., Englewood, N.J. 173 pp.

Kuerzi, R. G. 1941. Life history studies of the tree swallow. Proc. Linn. Soc., New York 52-53:1-52.

Lack, D. 1947. The significance of clutch-size. Ibis 89: 302-352.

_____. 1948. The significance of clutch-size. Ibis 90:25-37.

_____. 1954. The natural regulation of animal numbers. Oxford University Press, New York. 343 pp.

Lind, E. A. 1962. Verhalten der Mehlschevalbe, Delichon u. urbica (L.), zu ihren Feinden. Ann. Zool. Soc. Zool.-Bot. Fenn. "Vanamo" 23(5):1-38. (English summary).

_____. 1964. Nistzeitliche Geselligkeit der Mehlschwalbe, Delichon urbica (L.). Ann. Zool. Fenn. 1:7-43. (English summary).

MacNeill, N. 1954. Sand martins nesting in stonework. Irish Nats. J. 11:232.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1961. American wildlife and plants, a guide to wildlife food habits. Dover Publ., Inc., New York. 500 pp.

Merrill, H. 1881. Notes on a few Maine birds. Bull. Nut. Orn. Club 6:249-250. (Cited by Bent 1942).

Moreau, R. E. and W. M. Moreau. 1939. Observations on sand-martins at the nest. Brit. Birds 33:95-97.

Morlan, R. E. 1972. Predation at a northern Yukon bank swallow colony. Can. Field Nat. 86:376.

Oring, L. W., and M. L. Knudson. 1973. Monogamy and polyandry in the spotted sandpiper. Living Bird 12:59-74.

Palmer, E. L., and H. S. Fowler, 1975. Fieldbook of natural history, 2nd Ed. McGraw-Hill Book Co., N.Y. 779 pp.

Petersen, A. J. 1955. The breeding cycles of the bank swallows. Wil. Bull. 67:235-286.

Peterson, R. T. 1961. A field guide to western birds. Houghton Mifflin Co., Boston. 309 pp.

Potter, L. B. 1924. Badger digs for bank swallows. Condor 26:191.

Pough, R. H. 1957. Audubon western bird guide. Doubleday and Co., Garden City. 316 pp.

Purchon, R. D. 1948. The nesting activities of the swallow. Proc. Zool. Soc. London 118:146-170.

Reed, C. A. 1965. North American bird eggs. Dover Publ., Inc., New York. 372 pp.

Shortt, T. M. 1977. Wild birds of the Americas. Houghton Mifflin Co., Boston. 272 pp.

Snapp, B. D. 1976. Colonial breeding in the barn swallow (Hirundo rustica) and its adaptive significance. Condor 78:471-480.

Spencer, S. J. 1963. A study of the physical characteristics of nesting sites used by bank swallows. Dissert. Absts. 23(10):4034-4035.

Stoner, D. 1926. Observations and banding notes on the bank swallow-II. Auk 43:198-213.

_____. 1928. Observations and banding notes on the bank swallow. Auk 45:41-45.

_____. 1936a. Studies on the bank swallow Riparia riparia riparia (Linnaeus). Roos. Wldl. Ann. 4(2): 122-233.

_____. 1936b. Studies on the bank swallow, Riparia riparia riparia (Linnaeus) in the Oneida Lake region. Roos. Wldl. Ann. 9:173-177.

_____. 1937. Ten years' returns from banded bank swallows. N.Y. St. Mus. Circ. 18:1-21.

_____. 1938. Longevity in the bank swallow. Bird-Banding 9:173-177.

_____, and L. C. Stoner. 1941. Feeding of nestling bank swallows. Auk 58:52-55.

Sudhaus, W. 1970. Uferschwalben (Riparia riparia) als mauerbruter (bank swallows (Riparia riparia) using walls for breeding sites.) Ornithol. Mitt. 22(1):4-7. (English abstract).

Svensson, S. 1969. Hackingsbiologiska studier i en koloni av backsvala, Riparia riparia, vid ammarnas ar 1968. Var Fagelvard 28:236-240.

Taylor, D. W. 1948. Fundamentals of soil mechanics. John Wiley and Sons. New York, N.Y. 518 pp.

Thorpe, W. H. 1956. The language of birds. In: Readings from Scientific American-Animal behavior 1975. W. H. Freeman and Co., San Francisco. pp. 273-277.

Tinbergen, L. 1946. The sparrow-hawk (Accipter nisus L.) as a predator of passerine birds. Ardea 34:1-213.

Tinbergen, N. 1965. Social behavior in animals. Wiley and Sons, Inc., New York. 150 pp.

Torrey, B. 1903. Sand swallows (Riparia riparia) nesting in sawdust. Auk 20:436-437.

Witherby, H. F., F. C. R. Jourdain, N. F. Ticehurst and B. W. Tucker, 1940. The handbook of British birds. Vol II. Witherby; London. 374 pp.

Williams, P. L. 1967. Sand martins nesting in drainage holes by main road. Brit. Birds 60:167-168.

Windsor, D. and S. T. Emlen. 1975. Predator-prey interactions of adult and prefledging bank swallows and American kestrels. Condor 77(3):359-361.